

# EVOLUTIONARY TRENDS IN THE MARATTIALES

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## ABSTRACT

The structure of living and fossil marattiaceous ferns is compared organographically. Stellar structure exhibits a basic pattern in all genera in spite of modifications correlated with size and symmetry. Fronds exhibit gross morphological and anatomical differences but can likewise be interpreted as specializations associated with size and form, and genera can be related to one another in an evolutionary sequence. Living genera with dorsiventral stems and once pinnate or palmate fronds are considered derived from fossil forms with radially symmetrical stems and large, highly branched fronds. Primitive fronds had small pinnules which became modified into large laminar units in the living genera. Evidence from fossil and living genera is cited in support of these conclusions. The problem of sporangial aggregation is discussed in light of transformations in pinnule morphology. The linear sorus in the Pennsylvanian age *Eoangiopteris* is considered to have been produced on pinnatifid areas of *Psaronius*-type fronds. Other regions of the frond, or perhaps different fronds or plants, bore radially symmetrical synangia identified as *Scoleopteris iowensis*. The significance of this interpretation is the possible insight provided relative to the evolution of large laminar units and concomitant sporangial aggregation and distribution. *Senftenbergia* is rejected as a marattiaceous fructification.

The Marattiales is a distinct group of ferns restricted to tropical areas and consequently known to most North Americans only through occasional contact in conservatories or herbaria. The order is considered primitive among living ferns and, primarily because of their eusporangiate development, usually placed close to the Ophioglossales in taxonomic schemes. Most of the detailed studies of living genera were undertaken in the early years of this century, largely under the stimulus provided by the occurrence of fossil marattiaceous plants in Carboniferous strata. In recent years our knowledge of the fossil forms has accumulated in the virtual absence of further work with the extant genera so that once again we are in a position of lacking comparative data from the living representatives.

Seven extant genera have been described: *Angiopteris*, *Marattia*, *Archangiopteris*, *Protomarattia*, *Macroglossum*, *Christensenia*, and *Danaea*. Of these, *Angiopteris*, *Marattia*, *Danaea*, and *Christensenia* are the best known. Relatively little is known of *Archangiopteris* and *Macroglossum*, which contain only six species between them. No anatomical studies have been undertaken on *Protomarattia*, and it would be helpful to know how this genus compares with the other genera. (Copeland, 1947, in his *Genera Filicum* follows Christensen and Tardieu and places *Protomarattia tonkinensis* in synonymy with *Archangiopteris tamdaoensis*.)

The group is usually characterized as consisting of large, coarse, sappy ferns, the latter feature being a function of numerous mucilage canals and tannin cells in the fundamental tissue. The vascular anatomy, at least in the larger stems, is very complex, consisting of several interconnected cycles composed of small meristeles. Stems of some genera—*Angiopteris*, *Marattia*, and *Macroglossum*—are short, erect, tuberous and occasionally up to two feet in diameter. The remaining genera have trailing, mostly dorsiventral stems. All possess large

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fleshy stipules at the base of the petioles, and all genera exhibit circinate vernation. Fronds range in size from 6 m long with petioles 10 cm or more in diameter and supporting a lamina that may be four or five times pinnate, to much smaller once pinnate fronds. An even simpler frond is present in *Danaea simplicifolia* where the frond consists of a single blade. *Christensenia*, perhaps the most aberrant genus, has a palmate frond with radially symmetrical sori scattered over the abaxial surface of the pinnules. Sporangia are massive and are either free or fused into synangia depending upon the genus. All sori are linear except for the radial synangium of *Christensenia*. Gametophytes of five genera are known and are generally large, thick, dorsiventral, and similar to thallose liverworts in appearance.

Fossils attributed to the Marattiales occur abundantly in Carboniferous strata and consist almost entirely of various organ and form genera that represent the different parts of the plant designated by the genus *Psaronius*. *Psaronius* was one of the dominant plants of the Pennsylvanian period, and much of the fern foliage found on the spoil banks of North American coal mines was produced by this plant. There are a few reports of *Psaronius*-type plants from the Devonian (Dawson, 1871), but these reports need confirmation utilizing modern techniques before they can be accepted. *Psaronius* was abundant during the upper Carboniferous in Europe and America and ranged into the Permian of Europe. Mesozoic representatives of the group include six compression genera of sterile and fertile frond portions. Nothing is known about other parts of the plants, nor is there any anatomical information about the fronds. The laminar portions of most species are large, imparting an aspect similar to the fronds of living species.

In the strict sense *Psaronius* is a genus established in 1832 for structurally preserved fern stems, but has since come to indicate the entire plant in much the same way that *Lepidodendron* denotes one of the arborescent lycopods. *Psaronius* was a tall graceful tree fern, larger than the contemporary seed ferns but smaller than the giant lycopods. Growth began as a small sporeling (Stidd & Phillips, 1968) on the forest floor, where it must have encountered the usual problems other plants experience in becoming established in a forest. Like many ferns, and in particular the marattialean ferns, it was at first protostelic and with increase in size became siphonostelic and eventually developed a complex polycyclic dictyostele of unrivaled complexity in the plant kingdom. New cycles were added within the older cycles at successive heights as the plant grew upward. The entire complex stem was produced by the apical meristem, and even though it obtained a diameter of eight inches or more near the top of the tree, the tissues were all primary. Obviously a stem 50 feet tall, eight or more inches in diameter at the top, and supporting a crown of a dozen or more fronds, each of which was three meters or more in length, would need substantial supportive tissue in order to remain erect. This is particularly true when one remembers that the stem was only 1–2 mm in diameter at the base. Of course such a strange plant never existed, not even among the most bizarre fossil forms. The problem of support was solved by *Psaronius* in a unique way even more remarkable than the secondary growth mechanisms devised by arborescent monocots. Increase in circumference, and consequent supportive tissue, was accomplished



in *Psaronius* by the development of a layer of roots enveloping the stem. The root layer reached enormous proportions near the base of the plant, where the stem was very small, and diminished upward, giving a normal conical symmetry to the trunk. Individual roots of the root mantle were produced adventitiously at higher and higher levels as the stem increased in height. Roots originated primarily from the outer vascular cycle and passed outward to the stem surface. As the root apex approached the stem surface the subepidermal parenchyma of the stem began to proliferate and formed a tissue continuous with the cortex of the emerging roots. Subsequent roots arising at higher levels grew outward and downward over the previous roots and were also incorporated into the parenchyma matrix of the root mantle. In this way the stem increased in diameter by the addition of successive layers of roots forming a root mantle that was in actuality an integral part of the stem. Eventually the inter-root parenchyma failed to keep pace with new roots at the exterior, and the latter were not incorporated into the parenchyma matrix, thus forming the so-called free root zone.

The apex of the stem bore one or more whorls of large fronds with the characteristics of the form genus *Pecopteris*. Foliage of this genus has pinnules broadly attached at the base, parallel sides, and a single midvein entering the base of the pinnule. Lateral veins exhibited different forking patterns or were not forked at all. Fructifications were always synangiate and usually borne in two rows, one on either side of the midvein and directly beneath a lateral vein. Sporangia were massive, exannulate, and with one or two exceptions formed a radially symmetrical synangium. It was largely the presence of these fructifications in Carboniferous strata that was responsible for the widespread conviction that the Marattiales was well represented in the fossil record. With the discovery of the seed ferns, opinion for a time wavered (notably by Kidston, 1925) as to whether the fructifications were marattiaceous or represented the microsporangiate organs of pteridosperms. Today there is no question that the fructification genus *Scoleopteris* was borne on *Psaronius* fronds and that the genera *Eoangiopteris* and *Cyathotrachus* are marattiaceous. With a few exceptions then, the dozen or so genera described from the Carboniferous Period are in reality different parts of the plant designated by the name *Psaronius*. Consequently, a consideration of the relationships between the extant and extinct marattiales condenses primarily to the problem of how *Psaronius* is related to the seven extant genera. In spite of some obvious differences I am impressed by the similarities between *Psaronius* and the living genera, and the following organographic comparison reflects that bias.

#### STEMS

*Psaronius* stems were tall and were built up of multiple cycles of broad strap-shaped meristeleles embedded in the fundamental tissue. The complexity of the polycyclic dictyostele at higher levels in the plant defies comprehension by the casual observer. In extant genera such as *Angiopteris* the compactness of the stem plus the more dissected condition of the vascular tissue into smaller bundles makes interpretation equally difficult. If, however, one looks at the



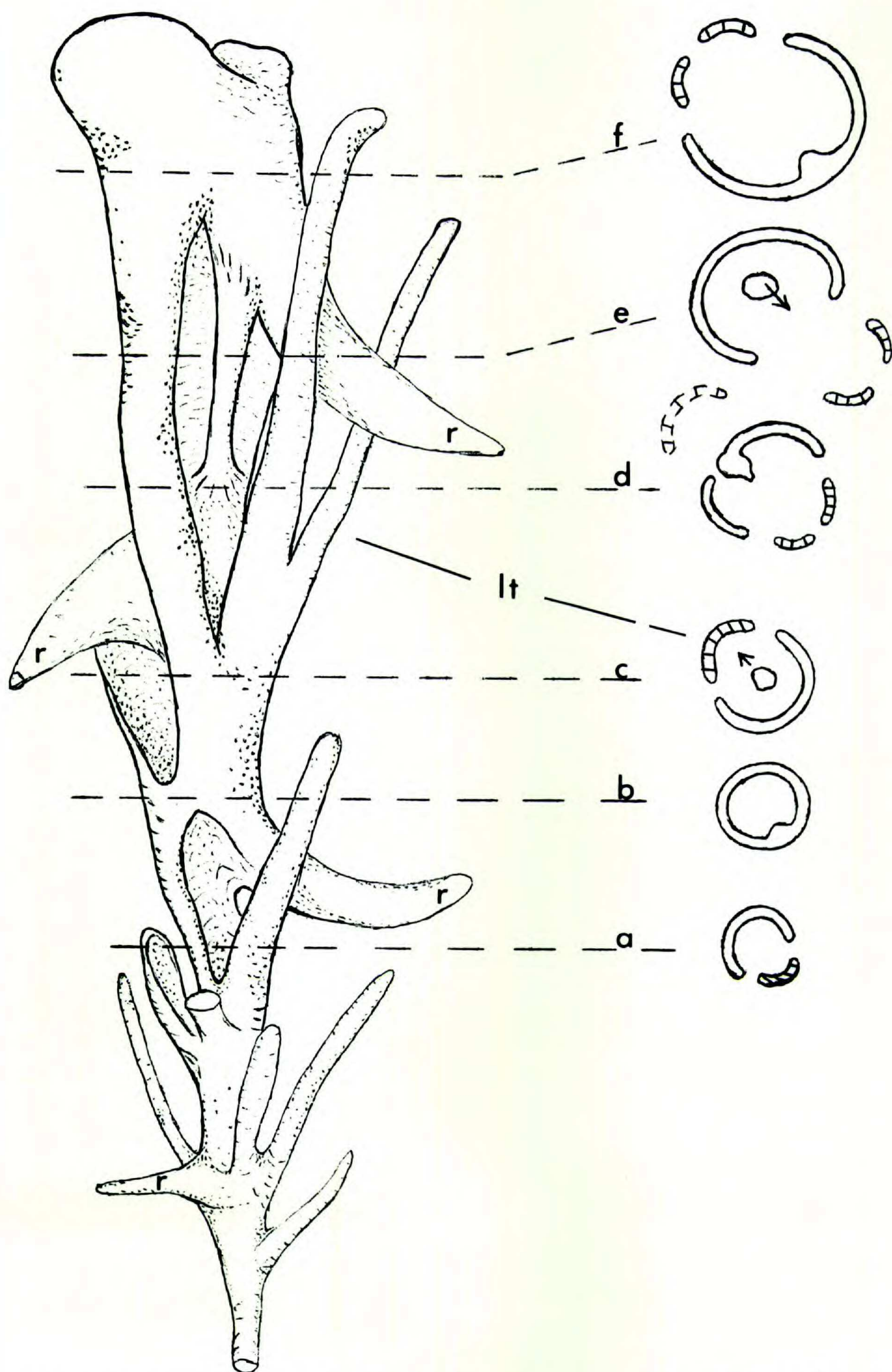


FIGURE 1. Drawing of the stelar system of the young sporophyte of *Danaea alata* (from West, 1917). Cross section diagrams supplied based upon description by West. Hatched segments are leaf traces.

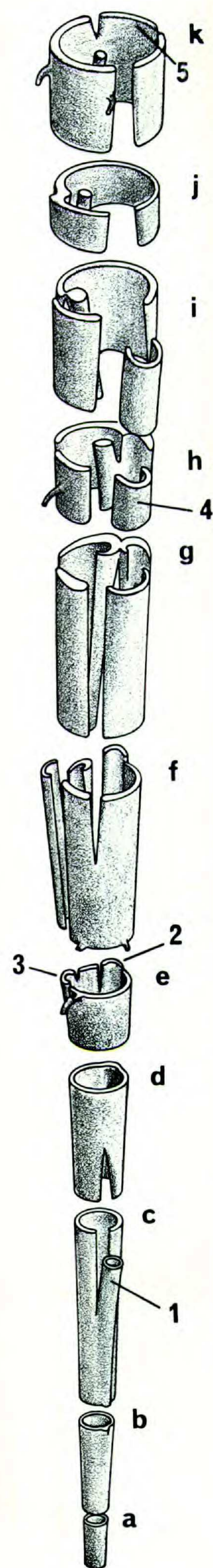


vascular system near the base of the plant before the bewildering array of meristeles of older stems develops, the basic nature of the vascular system is readily understood. Figures 1 and 2 show the vascular systems of *Psaronius* and *Danaea* sporelings. The cross sections of the *Danaea* stem have been supplied based upon the description of West (1917). In both genera a siphonostelic condition soon develops (Figs. 1a; 2a-b), and the first leaf gaps are closed by simple refusion of the edges of the gap (Fig. 2d). Eventually at higher levels, (Figs. 1b; 2g) gap-closure leaves a small amount of vascular tissue projecting to the inside. This tissue separates from the stele and at successively higher levels is found closer and closer to the next leaf gap in the phyllotactic sequence. This strand of vascular tissue represents the beginning of another vascular cycle inside the original siphonostele and has been called a commissural or medullary strand in the extant Marattiaceae and simply an internal strand or cycle in *Psaronius*. The internal cycle approaches the next leaf gap (Figs. 1c; 2h) and fuses with the edges of the gap near their point of convergence (Figs. 1d; 2i). In this way the internal cycle contributes to the closure of the leaf gap and subsequently separates and moves across the pith toward the gap created by the next leaf trace (Figs. 1e-f; 2j-k). Repetition of these events results in the internal cycle following an upward spiral course, anastomosing with the outer cycle at the top of each leaf gap. Eventually the internal strand becomes siphonostelic as the stem continues to increase in diameter, and only a portion of the strand is given off to the leaf gaps of the outer cycle. This of course creates gaps in the now tubular inner cycle. Some vascular tissue is eventually left to the interior of the second cycle when the vascular gap is closed by the free margins. This tissue functions and develops essentially as its predecessor (the second cycle at its origin), and a third internal cycle is created. In large stems of *Psaronius*, *Angiopteris*, and *Marattia*, many such cycles arise one inside the other and a complex polycyclic dictyostele results. Such a stelar structure may perhaps be comprehended by visualizing a series of perforated cones stacked one inside the other, each connected to the outer one at its point of origin and where gaps in outer cones are filled by contributions from inner cones.

Stem vasculature then, constitutes one of the distinctive characters of the Marattiales. Stelar anatomy of such complexity might be expected to exhibit considerable variability. For example in an account of the vascular anatomy of *Angiopteris* by Blomquist (1922) the term "commissural strand" is not used in the sense employed by most authors. The behavior of Blomquist's "commissural strand" is a good example of how a slight variation in vascular configuration masks the basic stelar pattern. In reality the specimen described by Blomquist exhibits the same basic stelar structure and development common to all genera. Many differences in stelar structure in the group are correlated with differences in size and symmetry between genera. Genera with larger stems (*Angiopteris*, *Marattia*) develop complex polycyclic steles, while those with small stems (*Danaea*, *Christensenia*, *Archangiopteris*) have less complex steles with only 2-3 cycles. Species with dorsiventral stems often have the stelar structure modified accordingly. The most extreme example is the genus *Christensenia* which has a strongly dorsiventral stem with leaves arising from the dorsal surface.



FIGURE 2. Vascular system of young sporophyte of *Psaronius*. 1-5 are leaf traces. From Stidd and Phillips, 1968.





The stem is dicyclic with a single internal vascular strand which follows an alternating course between the upper and lower edges of the outer cycle rather than the normal spiral course traversed by internal cycles in radially symmetrical stems. A very remarkable feature of the stele is the formation of gaps on the lower face of the outer cycle even though no leaf traces arise from the lower surface. This was interpreted by Farmer and Hill (1902) as evidence that the dorsiventral stem of *Christensenia* has been derived from a radially symmetrical ancestor.

#### FRONDS

Marattialean ferns possess megaphylls in the fullest sense of the term. The largest, most highly divided fronds occur in *Angiopteris*, *Marattia*, and *Psaronius*. The remaining genera have smaller once pinnate fronds with the exception of the palmate condition in *Christensenia*. *Macroglossum* fronds are once pinnate but up to 4 meters long and therefore perhaps the largest of the once pinnate fronds. *Danaea* is usually once pinnate, but one species, *Danaea simplicifolia*, has an even simpler frond with a single laminate blade (Fig. 7). *Psaronius* fronds were large, 3–4 times pinnate, and had many small, broadly attached pinnules imparting a lacey appearance to the frond. In contrast to the extant genera, there is no evidence that *Psaronius* had stipules.

A very interesting relationship exists between the vascularization and the size of the frond in the extant Marattiaceae. *Angiopteris*, which has the largest and most complex stem anatomy, also has the most complex vascular anatomy of the frond. Large petioles (Fig. 3a) have four or more concentric cycles of vascular bundles. The number of cycles is successively reduced as the distal end of the petiole and main rachis is approached (Fig. 3a–d). The vascular configurations in Figure 3b–d are repeated in primary pinna rachises, with the most complex configuration (Fig. 3b) present at the base of the pinna rachis. *Marattia* usually has a simpler vascular configuration at the base of the petiole (Fig. 3f) consisting of two or three vascular cycles. These are diminished distally in the rachis (Fig. 3g–h) in the same manner as in *Angiopteris* (Fig. 3b–d). This is accomplished by reduction of the inner cycle (Fig. 3b, f) to a single horizontally elongated strand (Fig. 3c, g) and finally by a series of fusions and separations of the horizontal strand with the bundles of the outer cycle at top-center (Fig. 3d, h) an open horseshoe configuration results as in Figure 3n. The smaller and less pinnate frond of *Danaea* has a simple vascular configuration in the petiole corresponding to more distal regions of the larger fronds of *Angiopteris* and *Marattia*. Either of two vascular arrangements (Fig. 3j or n) may be present in *Danaea* petioles.

The method of vascular supply to departing pinnae is a distinctive feature in the Marattiales. In all genera the vascular supply to pinnae is augmented by contributions from the vascular tissue in the interior of the main rachis. This is illustrated in Figure 3k, o where the vasculature is relatively simple. The bulk of the vascular tissue of the pinna comes from the bundles of the outer cycle. When an internal strand is present (Fig. 3k), vascular strands are constricted from the arms of the internal strand which contribute both to the bundles of the



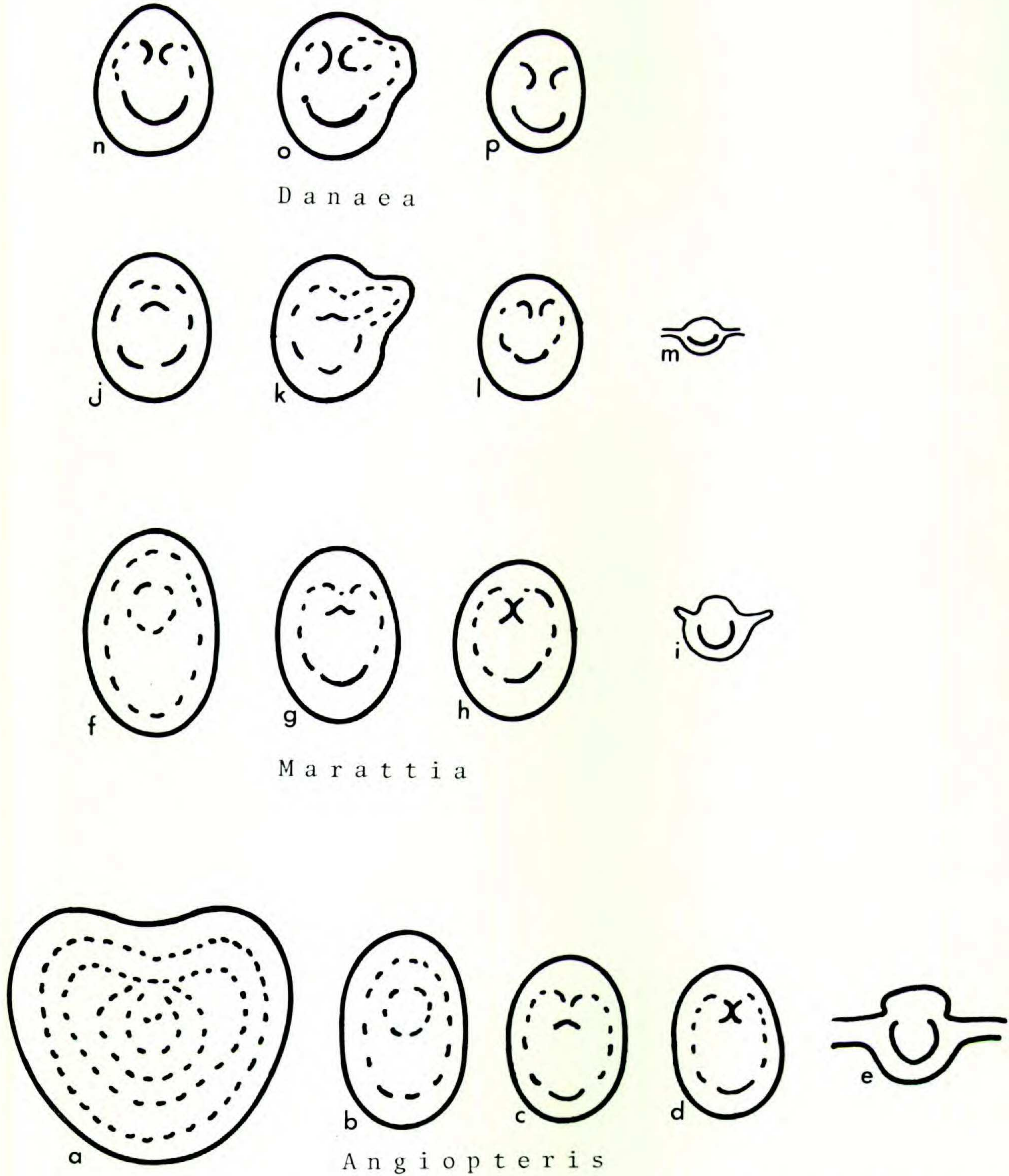


FIGURE 3. Transverse sections of frond members at selected levels of three extant genera. Solid outer line, edge of axis; broken lines, vascular bundles.

departing pinna and to the gap region created by the departure of bundles from the outer cycle. The internal strand in the frond functions in the same way as the internal cycle in the stem, *i.e.* it shifts from side to side along the length of the rachis, contributing vascular tissue to pinnae and closing pinnae gaps. It is not uncommon for the internal strand to divide and for the resulting halves to fuse with the two adaxial strands of the outer cycle. This results in a simpler vascular configuration with the bundles arranged as in a horseshoe but with the open ends slightly curved toward the center. When the bundles are arranged



in this way (Fig. 3o), a contribution to the pinna vasculature is made by the abaxially directed end of the incurved arm of the horseshoe. In this case (West, 1917) no bundles were observed to contribute to pinna gap closure.

The vascular configurations of the three genera illustrated in Figure 3 represent the range of vascular arrangements known among the extant Marattiaceae. The petioles of *Christensenia*, *Macroglossum*, and *Archangiopteris* have an outer ring of vascular bundles surrounding one or a few inner bundles, corresponding to the arrangement in other genera shown in Figure 3c, g, k. In the palmate frond of *Christensenia* this arrangement of bundles may be repeated at the base of the axes that support the large pinnules (Bertrand & Cornaille, 1902). This bundle arrangement is commonly transformed into the horseshoe configuration at more distal levels in the pinnule where the midrib is reduced in diameter.

*Psaronius* fronds were for the most part more highly branched than the living genera and bore many small pinnules attached broadly at the base. Adjacent pinnules are commonly fused together at the frond extremities resulting in a pinnatifid condition. Like the stem, the vascular tissue in the frond is composed of large continuous strands. At the base of the petiole the most common configuration consisted of an outer continuous strand enclosing a smaller internal strand (Fig. 4L). As in the living forms this vascular configuration is converted to the horseshoe configuration within the rachis and further interconversions between the two basic forms may occur throughout the length of the rachis. Primary, secondary, and tertiary pinna rachises usually have the horseshoe vascular configuration.

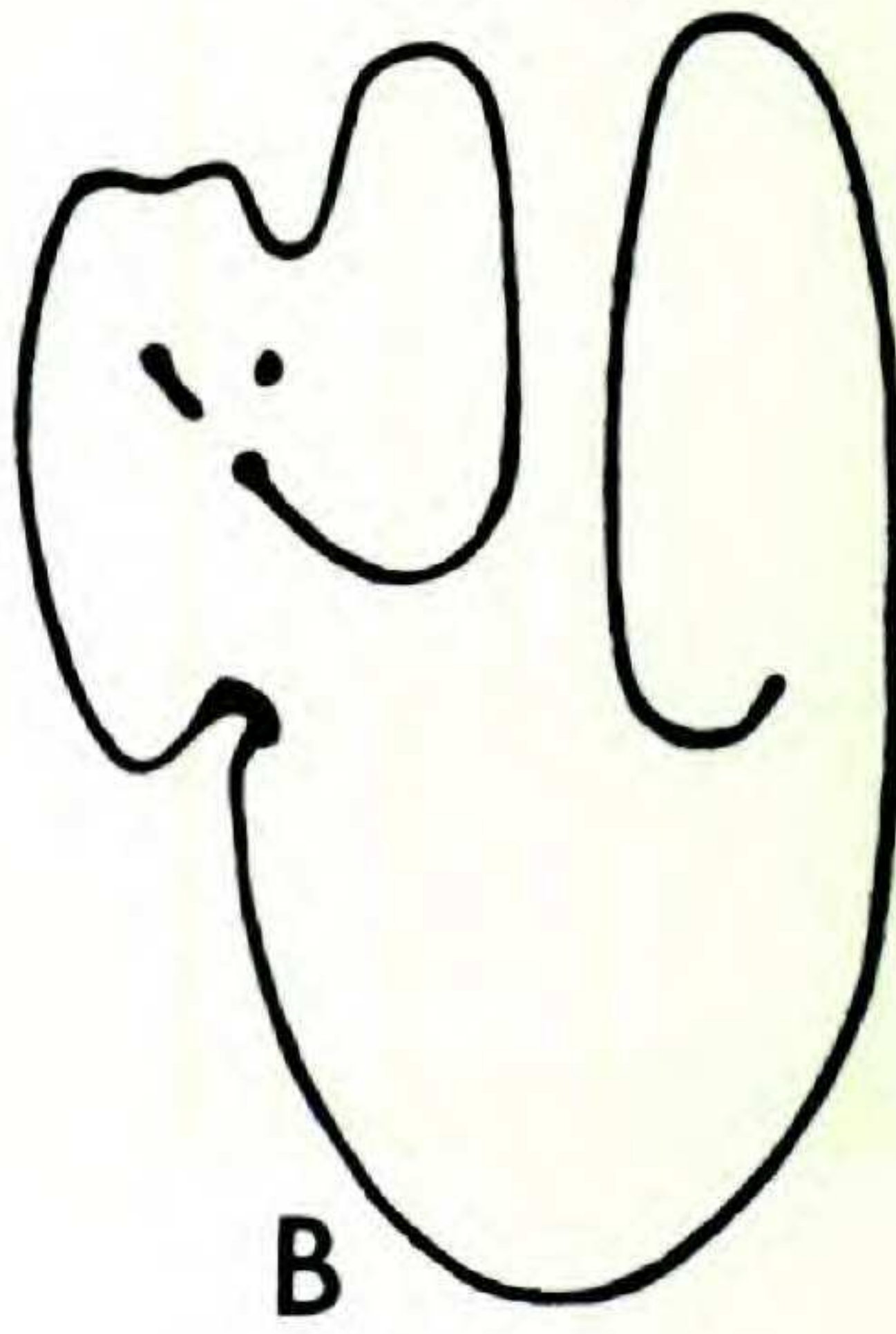
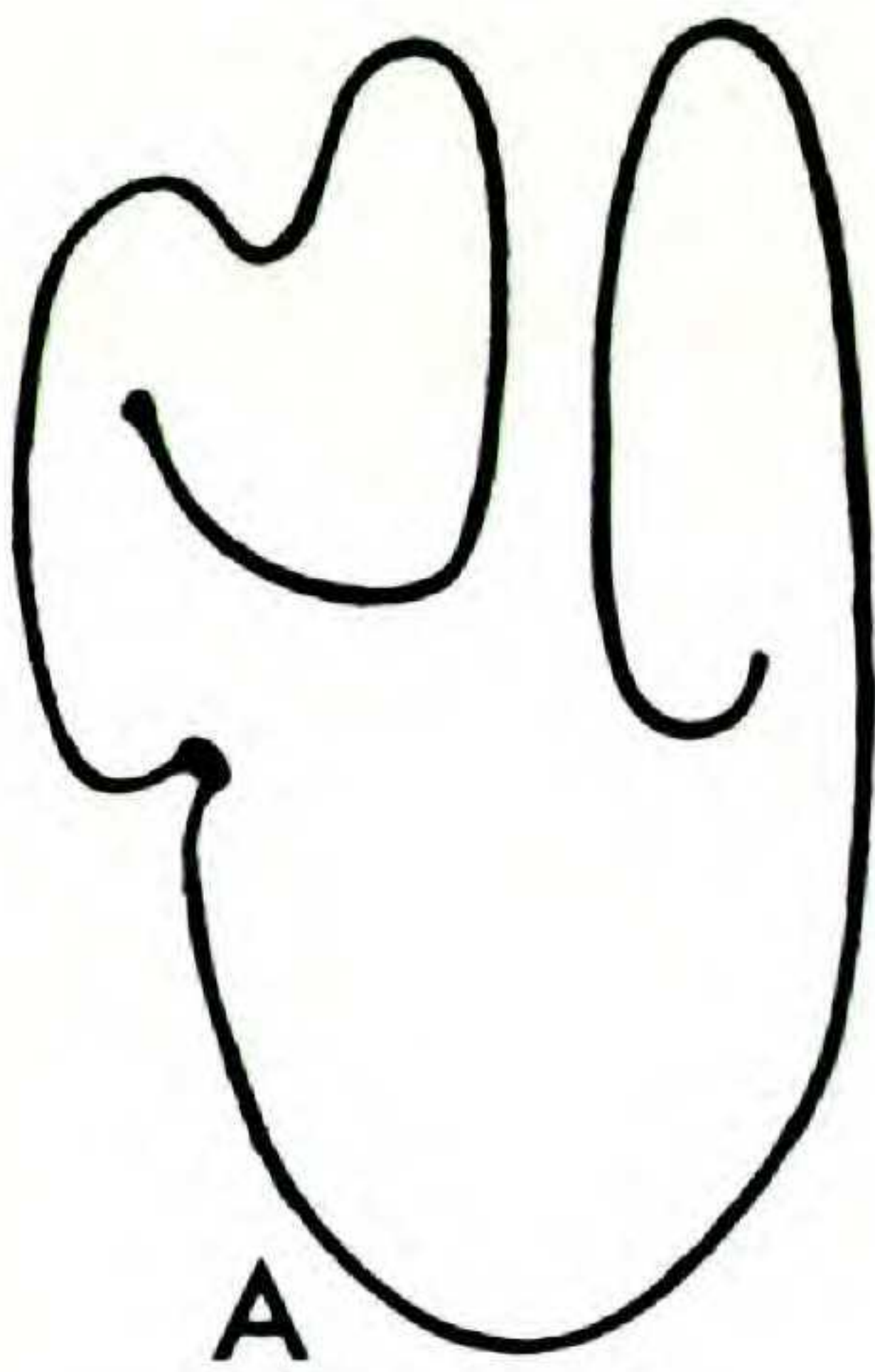
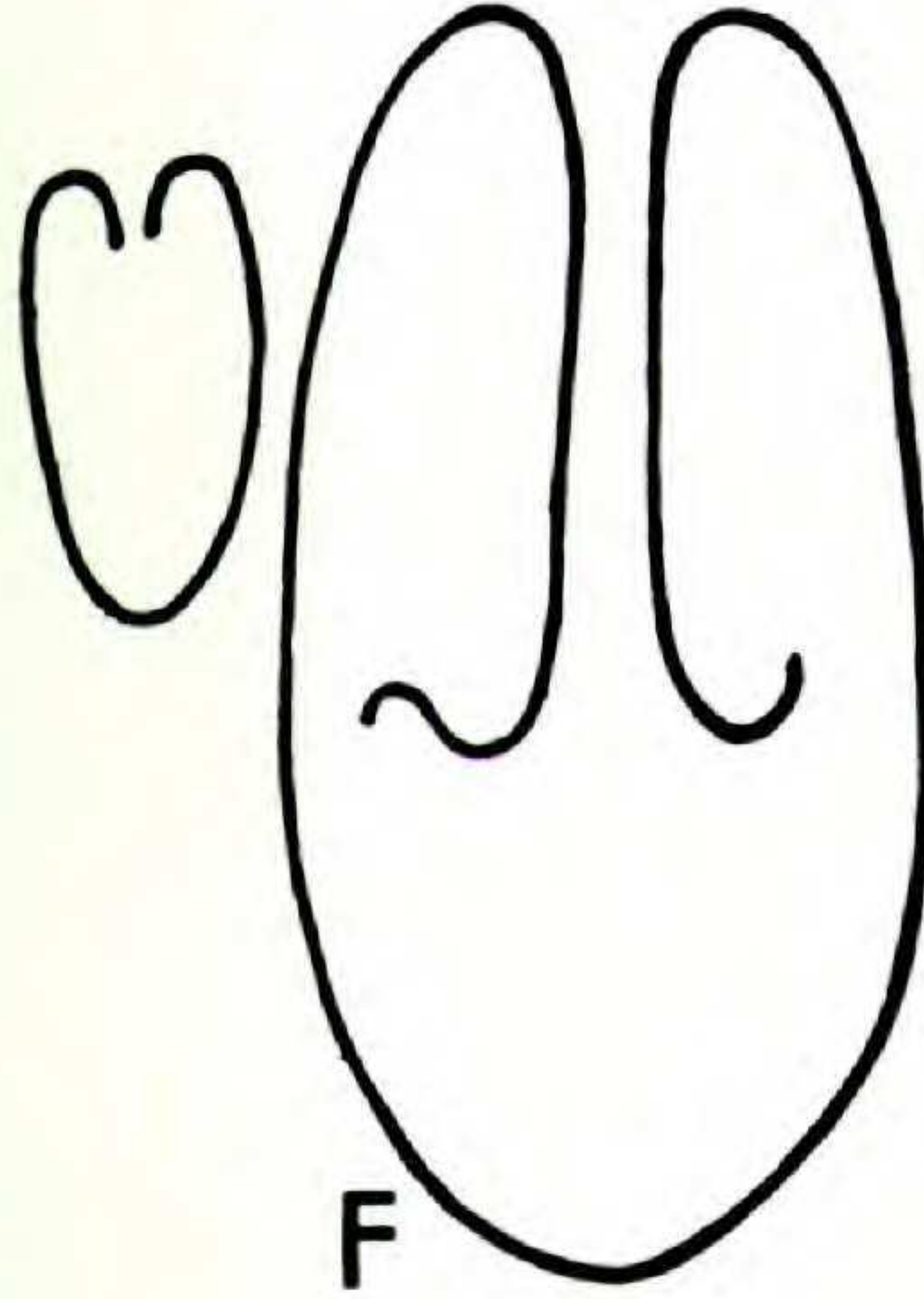
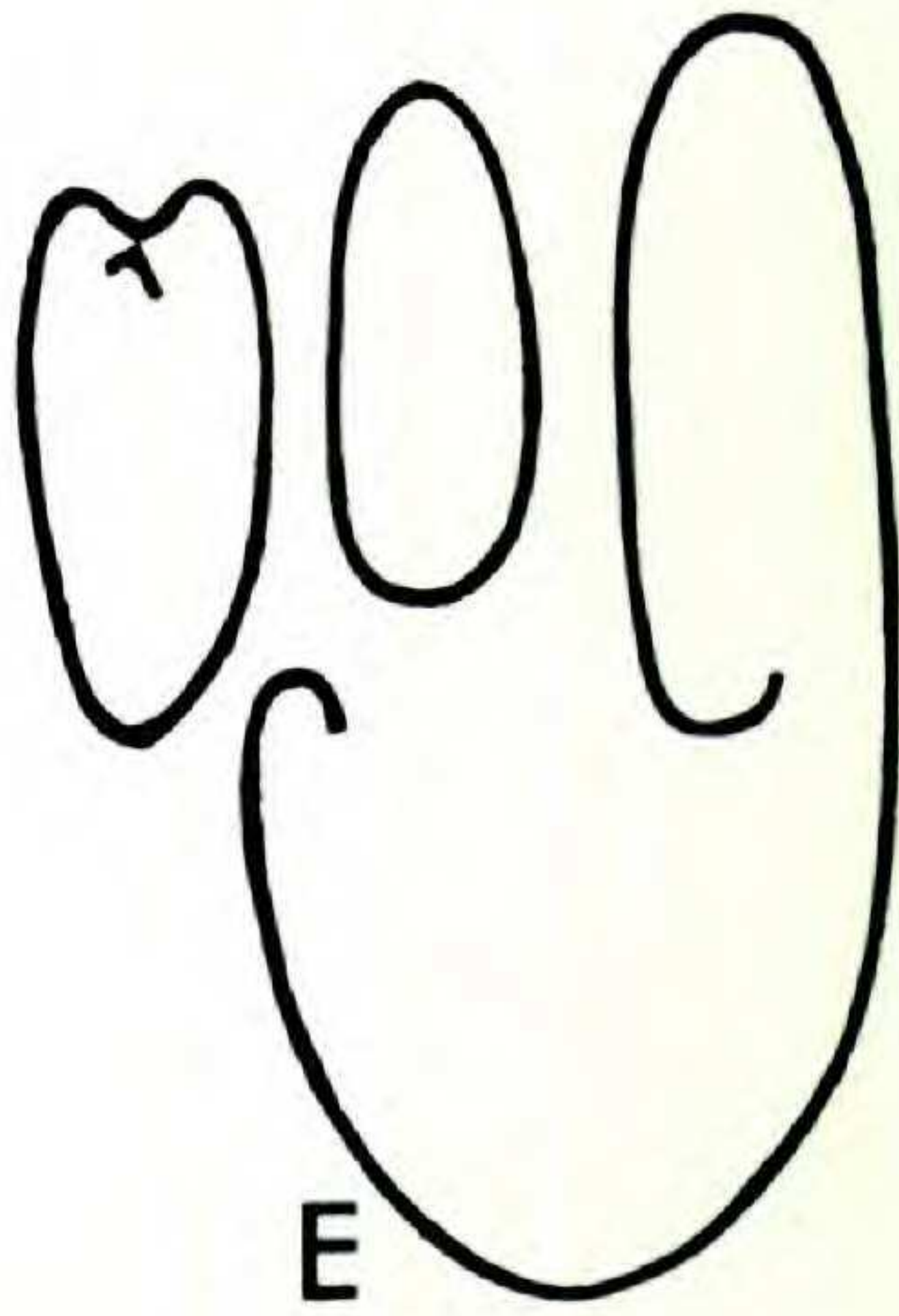
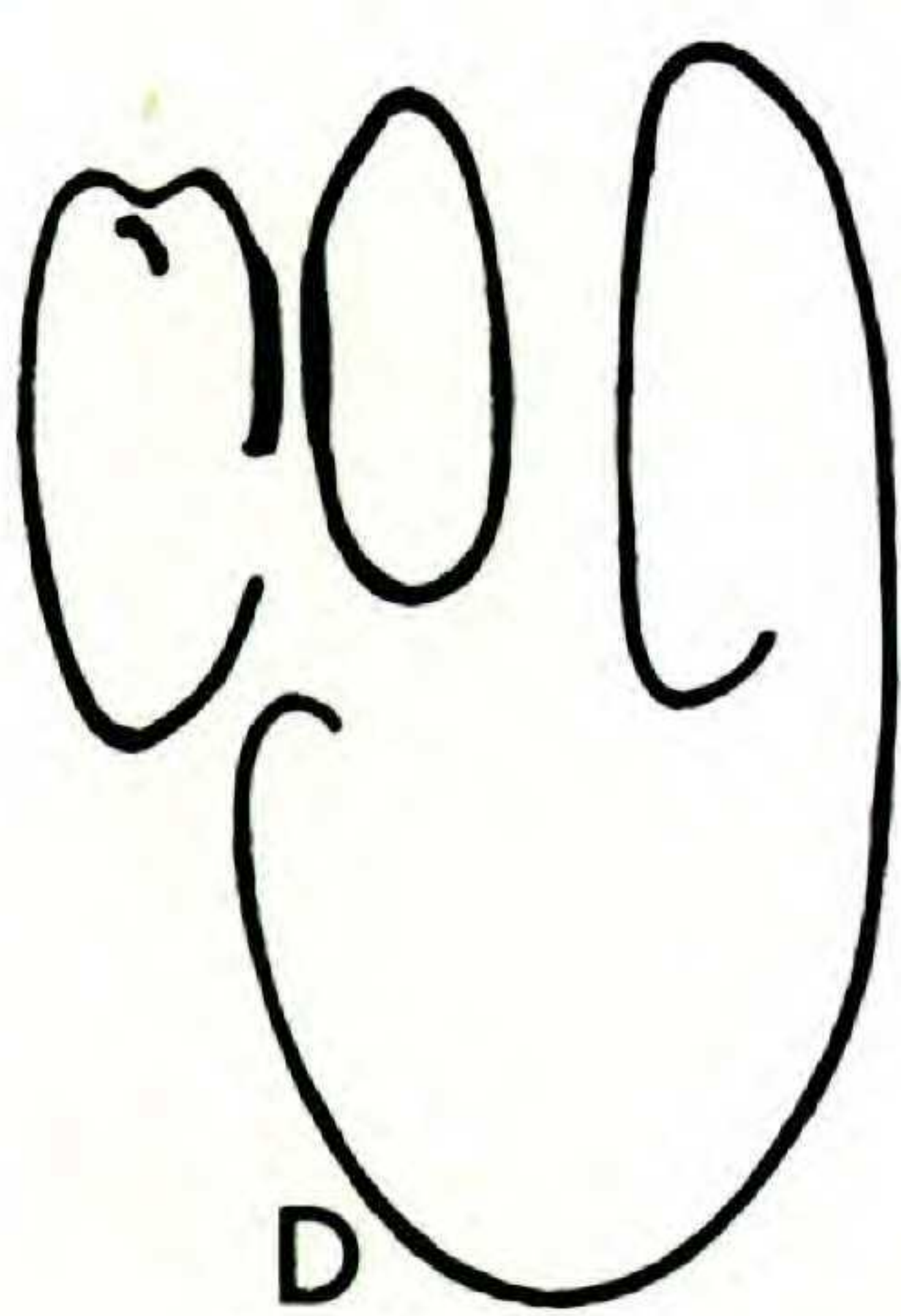
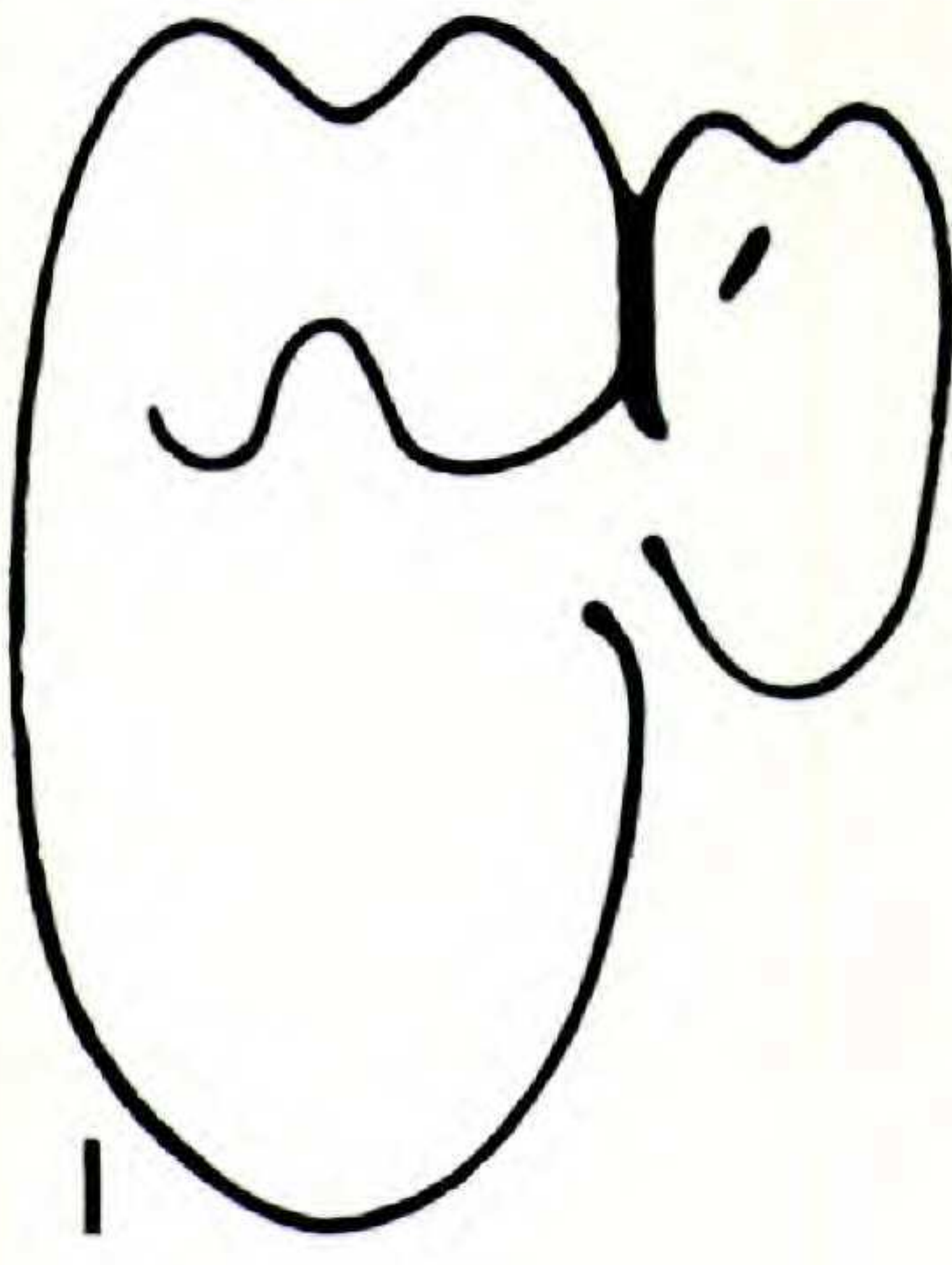
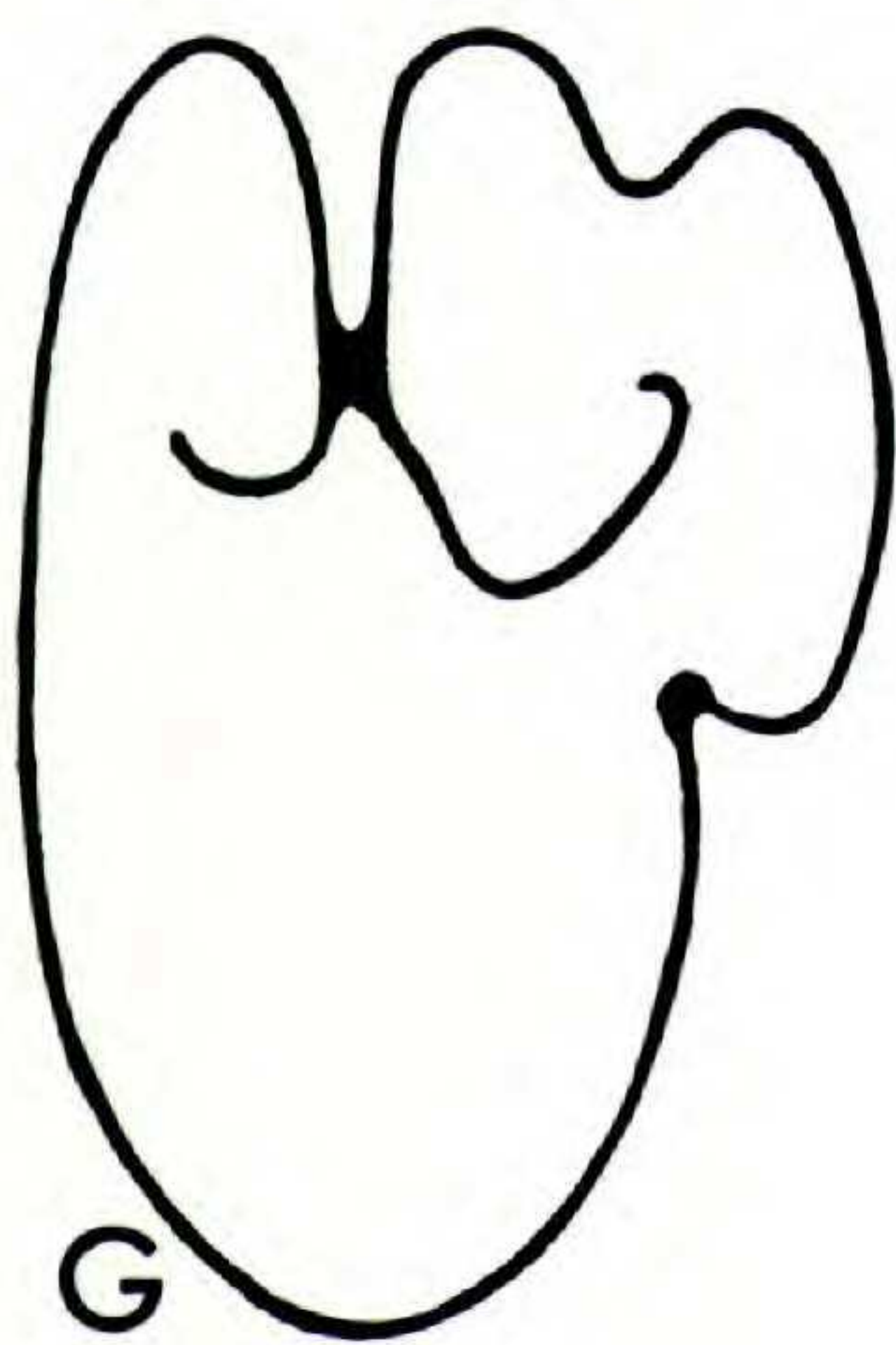
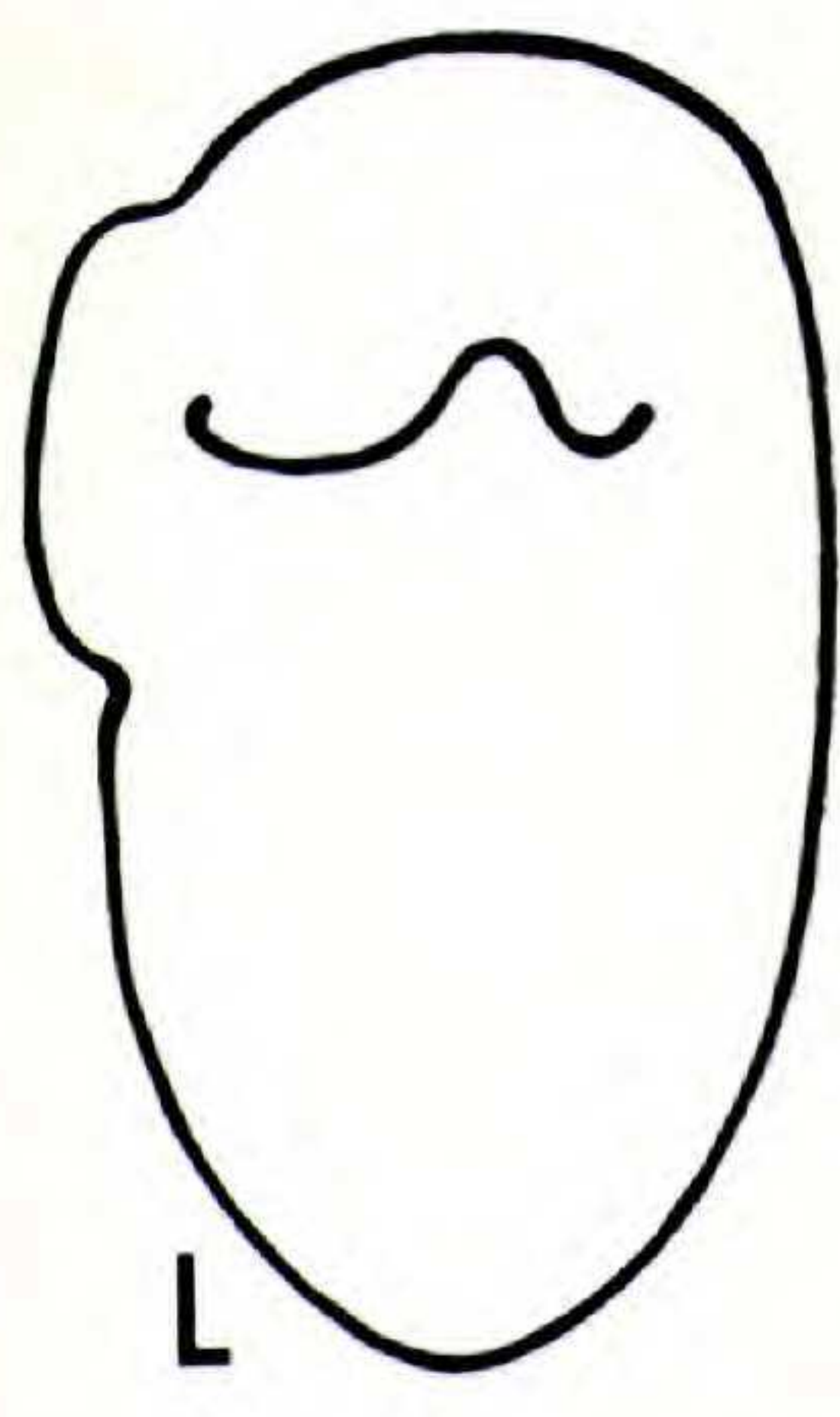
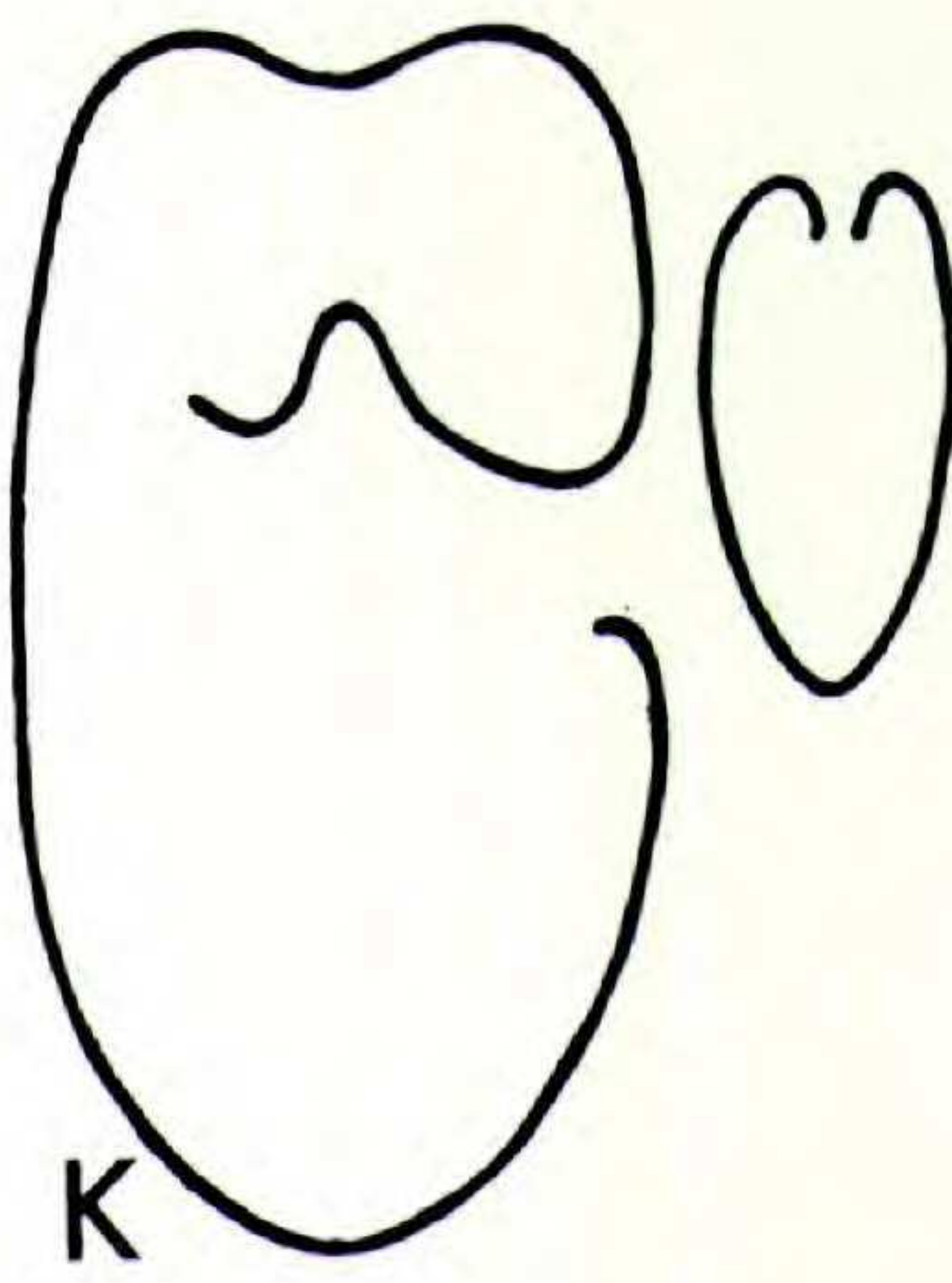
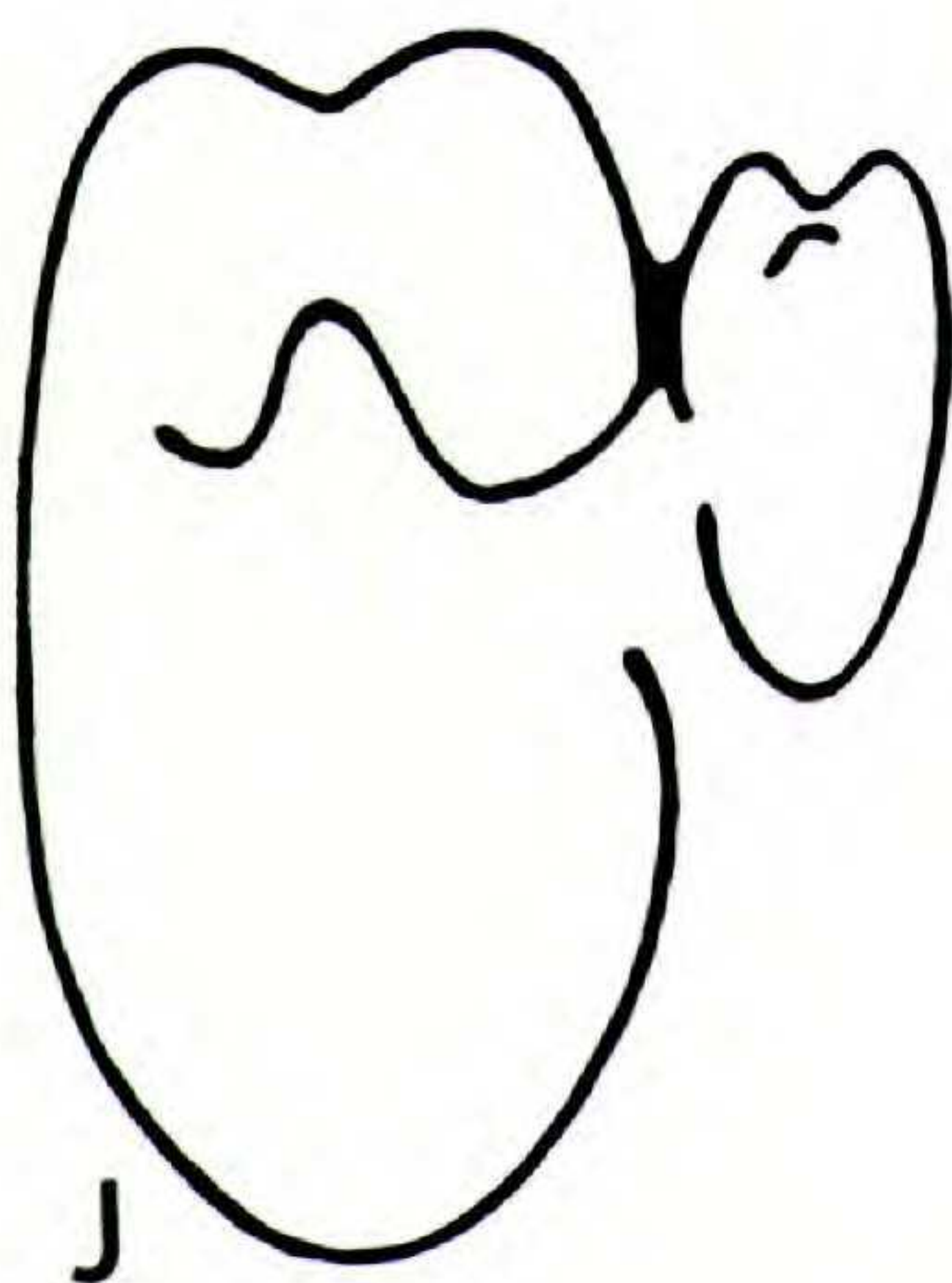
Pinna trace formation is augmented by contributions from internal vascular tissue as has been described for the living genera. When the vascular strand of the parent rachis is open at the top and no internal strand is present (Fig. 4F), the pinna vascular supply receives a small strand of vascular tissue from the recurved end of the adaxial hook of the parent rachis (Fig. 4A–E). In addition pinna gap closure is aided by further contributions from the same source. When an internal strand is present, as a result of fusion and subsequent separation of the enrolled arms of the vascular strand, pinna trace formation and gap closure is augmented by constrictions from the lateral extremities of the internal strand (Fig. 4 G–K). In this case the internal strand functions in a manner similar to the inner cycles in the stem except for the difference imposed by the bilateral symmetry of the frond.

At first glance the differences in the vascular system of *Psaronius* and the extant genera appear quite distinct. If, however, one connects the individual bundles in the living forms with a continuous line, the similarity with the vascular tissue in *Psaronius* is evident. The paths traversed and shifting of protoxylem positions of the individual bundles in the living genera is often made understandable by comparing with the changes in configuration of the continuous

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FIGURE 4. Selected transverse sections of rachis vascular system of *Psaronius* frond showing different vascular configurations and stages in pinna trace emission. A, most proximal level; L, distal.







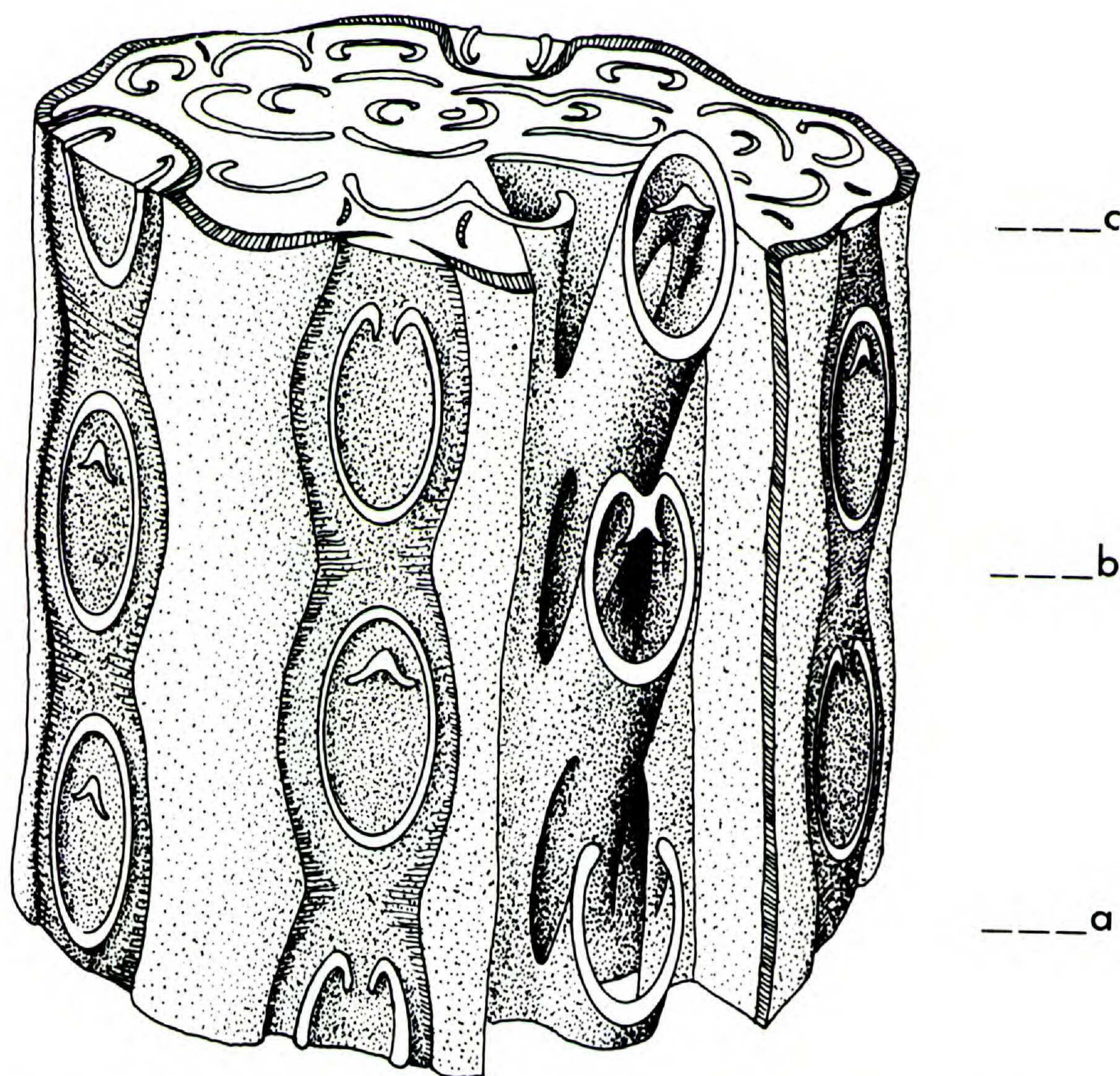


FIGURE 5. Segment of *Psaronius* stem showing origin of leaf traces (cut away portion). Levels a, b, c show three traces at successively greater distances from stem and different stages in the origin of the internal vascular strand at base of petiole.

vascular strands in *Psaronius*. For example, the following description of the course of vascular bundles in the petiole of *Christensenia* (Gwynne-Vaughan, 1905) is readily understandable to anyone familiar with how an internal strand is formed in *Psaronius* fronds: "These (vascular bundles) are arranged in a curve of the form of a widely open arch with its concavity facing directly towards the apex of the rhizome. The two terminal strands of the arch are somewhat larger than the rest, and as they pass upwards they approach the median plane of the petiole. As they do so they also curve inwards, and at the same time turn round so that their protoxylems face away from each other towards the sides of the petiole. This rotation is sometimes continued until at a point still further up their protoxylems face almost directly towards the median plane." There is no obvious reason why vascular bundles should rotate and shift positions as described here. However, if one conceives these bundles as segments of a once continuous vascular strand as in *Psaronius*, their otherwise peculiar behavior is explicable. Figure 5 depicts the way in which the internal strand is formed at the base of the *Psaronius* petiole. The internal strand (sometimes several



separate bundles) in the living genera is formed in the same way, but because the vascular tissue consists of individual bundles this was not always clear to earlier workers.

There are of course some differences between the vascular system of *Psaronius* and the living forms. One of the most inexplicable is the origin of so-called "accessory bundles" from normal bundles situated in the abaxial region of the petiole. These accessory bundles traverse the intervening ground tissue and join with the terminal bundles of the outer cycle (Gwynn-Vaughan, 1905). They may also form inner cycles in *Angiopteris* and *Marattia*. There is nothing about the vascular system of *Psaronius* fronds that provides any clues about the nature of these bundles. They are regarded therefore as a development peculiar to the living forms and perhaps in some way associated with the dissected nature of the vascular system.

How then should the similarities between *Psaronius* fronds and those of the extant genera be regarded? Certain features of *Psaronius* such as the integrated root mantle appear too specialized to allow *Psaronius* to be regarded as directly ancestral to the living forms. Nevertheless, comparative analysis of the living forms has caused some previous workers to regard the less compound fronds and dorsiventral stems as derived from plants with radially symmetrical stems and highly compound fronds. Since *Psaronius* has both radially symmetrical stems and large, highly compound fronds, and preceded the living forms in time, it is reasonable to conclude that *Psaronius* represents the ancestral form in at least some of its characters. If these assumptions are correct, the following changes in marattialean frond architecture may have occurred. Based upon certain theoretical considerations (Stidd, 1971) the primitive marattialean "frond" was probably a non-planated branching system possessing a radially symmetrical vascular system. The vascular system in such a frond probably resembled the vascular system of the stem in that internal cycles followed a spiral course in connection with pinna emission and gap closure. By the time *Psaronius* had evolved, the frond was distinctly planated and internal vascular tissue followed-suit, shifting from side to side in a bilaterally symmetrical fashion in connection with pinna emission. The vascular tissue in *Psaronius*, perhaps in response to its large size, consisted of a continuous strand of xylem and phloem in contrast to the distinct individual bundles in the living forms. The bundles in the living forms, however, are arranged in a definite manner that reflects the ancestral continuous strands as in *Psaronius*.

A second trend involved the fusion of small, individual pinnules borne on an ultimate pinna rachis into large laminar units. In such units the resulting midrib corresponds with, or is homologous to, the ultimate pinna rachis in the antecedent condition. Repetition of this process would result in decreasingly compound fronds, ultimately producing a simple frond with one blade (pinnule?) as in *Danaea simplicifolia*. A harbinger of this trend is the common pinnatifid condition near the extremities of *Psaronius* (*Pecopteris*) fronds. Apparently there is sufficient plasticity in the ontogenetic pathways controlling frond development in the Marattiales to allow frond axes to produce either discrete units (additional pinnae or individual pinnules) or solid laminar structures. An in-



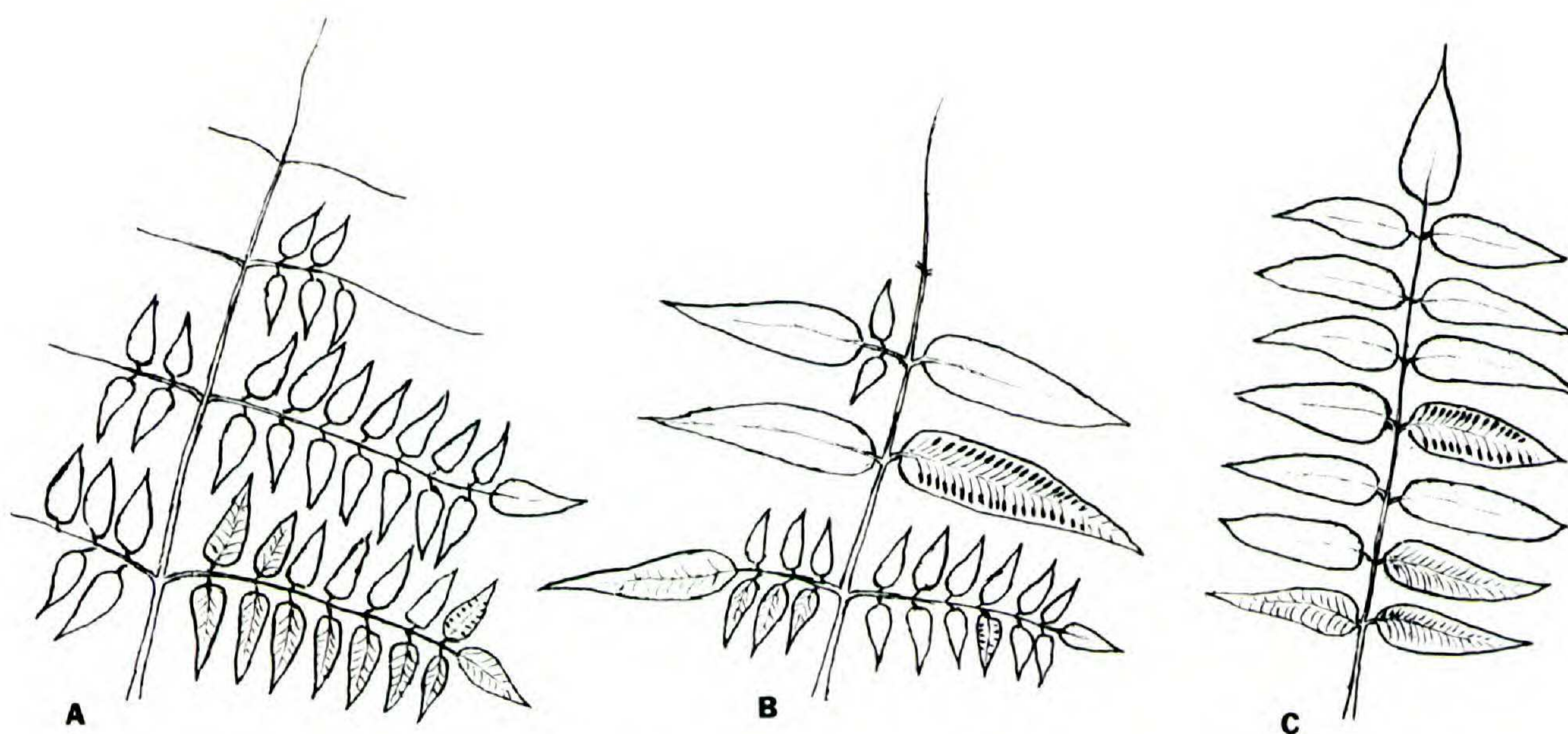


FIGURE 6. Diagrammatic drawings showing transformations in frond morphology of *Angiopteris lygodiiifolia* (See Asama, 1960).—A. normal frond development at Koshiki islands, 31°, 40' N latitude, 22.5° C mean temperature.—B–C. altered fronds when grown at Sendai, 37° 15' N latitude, 17.7° C mean temperature.

teresting example of this is the observations recorded by Asama (1960) on the transformations in frond structure of *Angiopteris lygodiiifolia* when transplanted 6 degrees northward, where growth conditions were less favorable. Under these conditions, plants with normal bipinnate fronds (Fig. 6a) produced fronds reduced in size and in some instances with fewer pinnae (Fig. 6b) each of which had fewer pinnules. Other fronds eliminated one order of branching and were once pinnate (Fig. 6c). In these fronds a pinnule was produced on the main rachis which corresponded in position to a pinna with pinnules in the normal bipinnate fronds. These changes were attributed by Asama to the reduced temperature which effected the fronds in early ontogenetic stages. *Cyathea boninsimensis* was also moved northward along with *Angiopteris* but underwent no noticeable changes in frond structure. The transformations exhibited by *Angiopteris lygodiiifolia* are of the same type as the postulated evolutionary changes depicted in Figure 7. It is conceivable that the changes in frond morphology outlined in Figure 7 were stimulated by the changing post-Pennsylvanian climatic conditions.

An interesting aspect of marattialean frond structure is the vascular anatomy at different levels in the frond. If the evolutionary trends suggested here are correct, then one might expect that where, in essence, a pinna rachis is converted into a pinnule midrib, the vascular configuration of the original pinna rachis might be retained. Information of this type is limited in the living forms and is a point that needs further investigation. One example, however, that illustrates the contention here and suggests the conservative nature of the vascular system is the arrangement of vascular bundles in the frond of *Christensenia*. Bertrand and Cornaille (1902) found that at the base of the pinnule an internal bundle is present, surrounded by an outer ring of bundles (Fig. 7). This configuration corresponds to that of Figure 3j and is the vascular arrangement



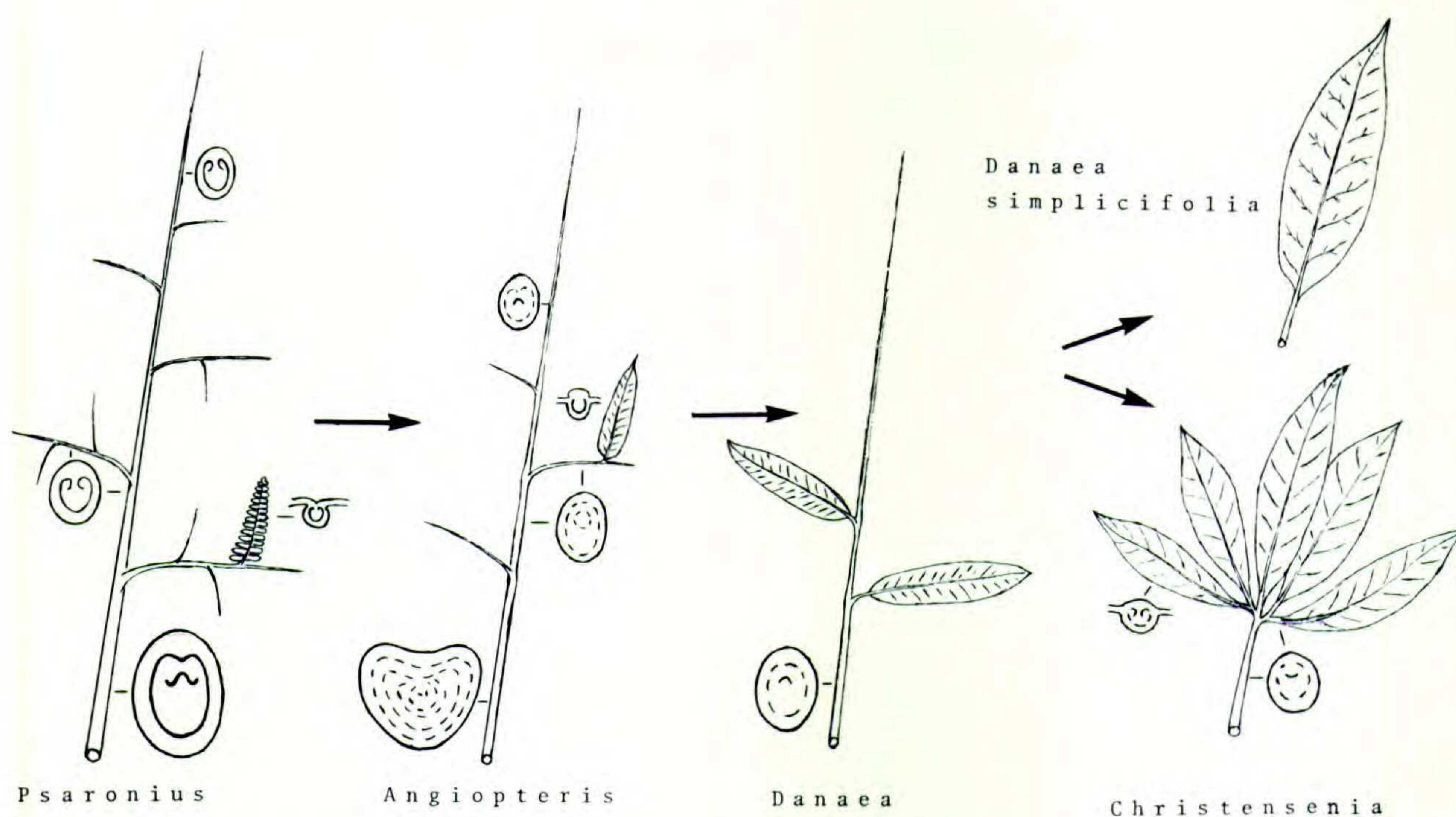


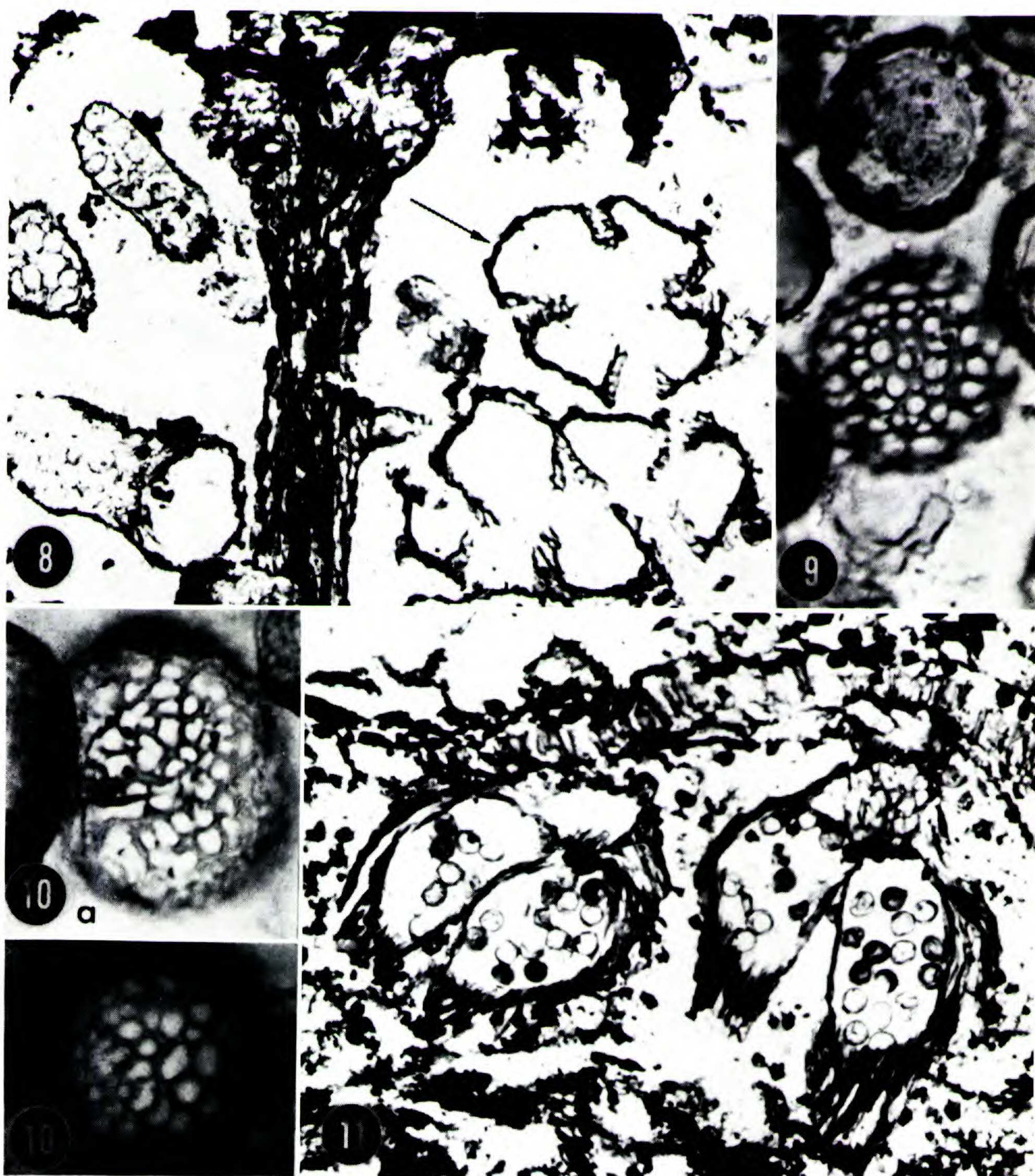
FIGURE 7. Schematic diagrams showing postulated evolutionary changes in marattialean frond morphology and anatomy.

that is normally present in a nonlaminated pinna rachis. Furthermore, the vascular configuration at the base of the pinnule is converted to a horseshoe arrangement of bundles toward the middle of the pinnule (Fig. 7). This is precisely the transformation that normally occurs in a pinna rachis or petiole in the genera with more highly branched fronds and is in distinct contrast to the terete vascular strand that traverses a pinnule of such a frond. It appears that although the morphology of the frond has changed drastically, the vascular anatomy has changed more slowly so that the midrib of the derived pinnule reflects its former state as a pinna rachis.

#### FRUCTIFICATIONS

Accepting for the moment the evolutionary trend in frond structure outlined in Figure 7, one might ask how soral distribution was affected by the appearance of large laminate pinnules concomitant with fewer branching orders. My initial thoughts were that fusion of small pinnules laterally would have brought their sori into close proximity and fusion of circular sori (*Scolecopteris*) might have resulted in the linear sori so predominant in the living genera. A similar sequence of events was suggested by Mamay (1950); *Scolecopteris iowensis*, which sometimes has two series of circular sori on each side of the pinnule midrib, was considered to have produced the linear sorus of *Eoangiopteris* by fusion of two sori borne on the same lateral vein. Any such scheme, however, presents certain spatial and geometric problems involving orientation of the resulting linear sorus in relation to the midrib and pinna rachis. Such schemes also ignore developmental aspects of the production of large laminar units replacing a series of individual small pinnules borne along an ultimate pinna rachis. Again the changes in frond morphology observed by Asama in *Angiop-*





FIGURES 8-11. Sporangia and spores of *Eoangiopteris* and *Scolecopteris iowensis*.—8. Paradermal section of pinnule of *E. andrewsii* through synangial receptacles on left, midrib in center, and sporangia on right. Note the radially symmetrical synangium at arrow.  $\times 50$ .—9. Spores of *E. andrewsii*.  $\times 500$ .—10a-b. Spores of *S. iowensis*  $\times 500$ .—11. Longitudinal section through two synangia of *S. iowensis* attached to pinnule above.  $\times 50$ .

*teris* are pertinent to the question of soral arrangement. When a pinna rachis with individual pinnules is transformed into a large, wide foliar unit (enlarged pinnule), the sori have the same relative distribution and arrangement on the enlarged, derived pinnule as on the smaller antecedent pinnules, *i.e.* near the edge of, and at right angles to, the margin. The transformation occurs abruptly without passing through a series of intermediate stages. If the evolution of the Marattiales proceeded by quantum steps of this sort, we would not expect to find a complete series of intermediate forms in the fossil record.



With these considerations in mind, it seems reasonable that the fossil fructifications *Scolecopteris iowensis* (Fig. 11) and *Eoangiopteris* (Fig. 8) represent a transformation of foliar and fructification units similar to the morphological changes observed in *Angiopteris lygodiifolia*. It is unfortunate that we know so little about the plants that bore *S. iowensis* and *Eoangiopteris*, but the pinnule structure and anatomy of the ultimate pinna rachis indicate *Psaronius* as the parent plant. It is possible that the two fructifications in question were borne on the same plant and perhaps even on the same frond. The similarities between *Scolecopteris iowensis* (radial sorus) and *Eoangiopteris* (linear sorus), in spite of the difference in symmetry, are striking and were well summarized by Mamay (1950): "Referring back to the description of *Scolecopteris iowensis*, a radial sorus, and *Eoangiopteris andrewsii*, a linear sorus, certain similarities may be noted between the two fructifications. Individual sporangia of the two are similar in size, shape, and their dehiscence mechanisms. The tissues comprising the pedicel of *S. iowensis* and the receptacle of *E. andrewsii* are alike. The spores of the two compare closely in gross morphology, size, and sculpturing of the exine. The chief difference between the two lies in the radial aspect of one as opposed to the linear aspect of the other." If the suggestion outlined above is correct, the difference between radial and linear sori are just what one might expect if the respective fructifications were borne on a plant undergoing changes in frond morphology. Further considerations, in part based upon study of the type material, can be interpreted in support of the suggestion that the two fructifications represent one taxon. First, the fertile pinnule of *Eoangiopteris* is slightly larger than most fertile pinnules of *Scolecopteris*. In this regard it should be noted that the "midrib" of *Eoangiopteris* is described as having a U-shaped vascular bundle. All species of *Scolecopteris* have a small terete vascular bundle traversing the midrib, and it is the pinna rachis bearing the pinnules that has a U-shaped vascular bundle. The interpretation suggested here is that *Eoangiopteris* represents an enlarged pinnule derived from ontogenetic fusion of smaller pinnules and that the "midrib" is in reality the former ultimate pinna rachis. Accordingly, the transformed midrib contains a U-shaped vascular strand reflecting its former status. Secondly, not all the sori of *Eoangiopteris* are linear. Figure 8 shows a radial sorus near the tip of a pinnule adjacent to a linear sorus. Such a sorus is scarcely distinguishable from *S. iowensis* and is further evidence that *S. iowensis* and *Eoangiopteris* are not generically distinct. The similarity of spore size and wall structure is a third reason for considering *S. iowensis* and *Eoangiopteris* as merely different forms of the same structural unit. *Scolecopteris iowensis* spores (Fig. 10a, b) are distinctly larger than other spores in the genus but only slightly larger than those of *Eoangiopteris* (Fig. 9). The spores of both are thick walled and have distinct pits in the exine. These features readily separate *S. iowensis* from other species of *Scolecopteris* and support the contention that *S. iowensis* and *Eoangiopteris* are conspecific. According to this interpretation then, one would expect to find in the same biological species, sporangia borne in the three ways exhibited by *S. iowensis* and *Eoangiopteris*, i.e. either in a single or double series on either side of the midrib or in linear synangia as in *Eoangiopteris*. Figure 12 illustrates some of the possible ways



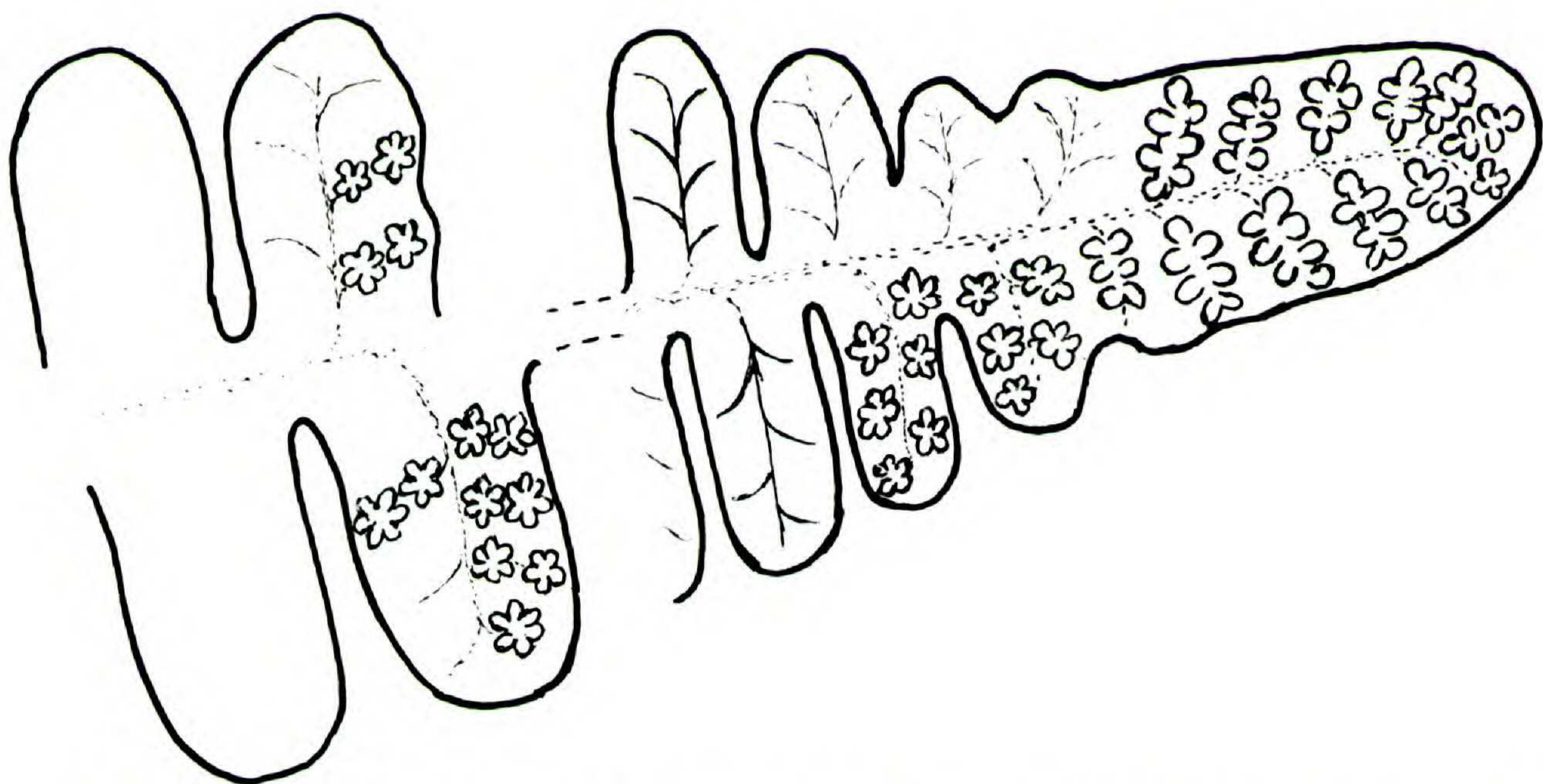


FIGURE 12. Sketch showing hypothetical distribution of *Scolecopteris iowensis* and *Eoangiopteris andrewsii* on *Pecopteris* foliage. Double and single series of synangia on each side of midvein of *S. iowensis* at left and middle respectively. *E. andrewsii* on terminal pinnule at right.

sporangia might be aggregated and is offered only as an aid in visualizing the suggestions made above. It is recognized that the possibilities represented in this sketch might not occur on one portion of a frond nor even necessarily on the same plant. The significance of this suggestion is the insight provided concerning possible sporangial aggregation and pinnule fusion in a species of Carboniferous age.

#### DISCUSSION

One of the most obvious problems in a consideration of the evolution of the marattialean ferns is the fact that there are few clues as to how the group might have originated. From its very first appearance in the Carboniferous *Psaronius* possesses a very distinct, even unique, morphology and anatomy. It is very difficult, on the basis of our current information, to detect evolutionary relationships *within* the genus. We need to know more about the Devonian specimens attributed to *Psaronius*. We need more information about the plant or plants that bore *S. iowensis* and *Eoangiopteris*. The genus *Radstockia* (Taylor, 1967) is an intriguing compression fossil known in this country from the famous Mazon Creek locality. The linear synangia appear nearly identical to those in the living genus, *Marattia*. The occurrence of a Carboniferous form with such striking similarities to an extant genus and contemporaneous with the genus *Psaronius* suggests the existence in Carboniferous time of marattialean forms much more like the living forms than *Psaronius*. We may hope that future discoveries provide more information about the plant that produced the fertile regions of *Radstockia*.

*Psaronius* then is perhaps best regarded as an early representative of the Marattiales which was well adapted for survival in the Carboniferous swamp forests. The geologic and consequent environmental changes which accompanied the Permian and later periods were too drastic for *Psaronius* and most other



species of the period. Many were highly specialized and adapted to the unique environment of the time and grew and multiplied in great numbers. This is reflected in the frequency with which they are encountered as fossils. What we learn of these plants greatly increases our understanding of the various taxa that they represent but as often as not more questions are raised than answered. The modern survivors of the fossil forms were in most cases probably not derived from the dominants but more likely from plants less well adapted to the prevailing conditions and therefore less numerous. The latter were able to adapt to the changing conditions of subsequent environments. The rare occurrence of *Radstockia* indicates that other marattialean forms were present but were much less numerous than the dominant *Psaronius* and are consequently much more poorly represented in our fossil collections. Unfortunately, if this conjecture is true, the critical specimens needed to determine the phylogeny of the Marattiales are perhaps forever beyond our grasp. The presence of *Radstockia* and *Psaronius* in Carboniferous strata presents us with two contemporaneous fossil forms with distinct differences in morphology and synangial type. Each appears too specialized to be ancestral to the other genera, and we therefore must await future discoveries to resolve the ancestry of the group.

What then can be said about the evolution of the Marattiales and upon what bases are relationships to be determined? The answer to the second part of the question is that at present one must rely on the classic methods of comparative morphology and anatomy. In such an attempt we are confronted with at least two fossil members and six or seven living genera. The fossil members *Psaronius* and *Radstockia* are each specialized in their own way; *Psaronius* with a tall erect stem and unique supporting root mantle and *Radstockia* with unknown stem but with linear synangia much more specialized than the radial synangia of *Psaronius*. Bierhorst (1971) has suggested that in the Marattiales the free sporangiate condition is derived from a synangiate one. The occurrence of linear synangia as in *Radstockia* contemporaneously with *Psaronius* is evidence that both conditions had evolved by Carboniferous time and is not helpful in deciding which was the primitive condition. If the contention is correct that the linear synangium of *Eoangiopteris* is a modification and fusion of radially symmetrical synangia in response to morphological changes in the laminar surface of the frond, then we see a rare instance of how a developmental aspect of one species provides clues to pathways which may have occurred in the evolution of the larger group. Sporangial aggregation has apparently evolved in different ways in descendant genera. In *Macroglossum*, *Archangiopteris*, and *Danaea* linear synangia represent one extreme, while in *Christensenia* the radial sorus was retained and became scattered over the surface of the large laminar units. *Christensenia* is regarded as highly modified from the ancestral condition in its vegetative anatomy and morphology but has retained the presumed primitive type of synangium. The trend in frond morphology outlined in Figure 7 is not to be interpreted as suggesting that the illustrated genera were derived from each other. Rather it is intended to illustrate broad evolutionary tendencies in frond morphology which probably occurred within as well as between genera. Some evolutionary trends in the Marattiales are summarized in Table 1.



TABLE 1. Some evolutionary trends in the Marattiales.

Character	Primitive	Derived
Stem anatomy.	Protostelic—Siphonostelic; strap-shaped vascular bundles.	Polycyclic, dictyostelic; small individual vascular bundles.
Stem morphology.	Erect, radially symmetrical.	Prostrate, bilaterally symmetrical.
Roots.	One root/leaf.	Root mantle in <i>Psaronius</i> ; no association between roots and leaves.
Frond morphology.	Large, highly divided; small pinnules.	Large pinnules, once pinnate or less.
Frond anatomy.	Many bundles.	Few vascular bundles.
Fructifications.	Radially symmetrical sorus, free sporangiate.	Linear sorus, synangiate.

One of the problems in assessing evolutionary trends in the Marattiales is determining the effects of size on form and anatomy. For instance, the broad strap-shaped vascular bundles in *Psaronius* may indicate an adaptation to the large size of the plant and not a primitive condition as indicated in Table 1. Large fronds of a given taxa tend to be more highly divided than small fronds. Size and form are so closely correlated in the Marattiales that size alone is perhaps a primary evolutionary factor and consequent anatomy and morphology secondary.

A concluding note on the classification and taxonomy of the Marattiales is in order. Certain French workers have for some time contended that the fructification genus *Senftenbergia* is borne on *Pecopteris* foliage which was in turn borne on the arborescent trunks known as *Megaphyton* (Dalinval, 1960). *Megaphyton* is a *Psaronius*-type stem distinguished by the presence of two rows of leaf scars on opposite sides of the stem. Moreover, the vascular system of the leaf scar shows various stages of division indicating that the frond bifurcated near its base. *Senftenbergia* is a very unmarattiaceous type sporangium that has been allied with the Schizeaceae because of its apical annulus. Also, sporangia are not grouped into sori as in the Marattiales. The contention that *Senftenbergia* represents the fertile regions of *Megaphyton* is such an unlikely possibility that such a conclusion must have strong supporting evidence and in my opinion has not been provided. Recent work by Jennings and Eggert (1972) casts serious doubt on either a marattiaceous or schizaeaceous affinity of *Senftenbergia*. Their evidence suggests that *Senftenbergia* belongs to an *Ankyropteris*-type plant.

The Marattiales appear then as a distinct group of plants with sufficient similarity to be included in one family in spite of the gross differences in habit, for example, between the fossil *Psaronius* and the living *Christensenia*. The same structural plan is present in all members, and the extremes in morphology and anatomy are for the most part readily interpretable as specializations of a basic type. But as in so many other taxa, despite a good fossil record, the ancestral type remains a mental concept.



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